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RESEARCH ARTICLE

Estimating egg mass–body mass relationships in birds

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ABSTRACT

The mass of a bird's egg is a critical attribute of the species' life history and represents a fundamental component of reproductive effort. Indeed, the tradeoff between the number of eggs in a clutch and clutch mass lies at the heart of understanding how environmental attributes such as nest predation or adult mortality influence reproductive investment. However, egg masses have not been reported for the majority of avian species. We capitalized on the strong allometric relationship between avian body mass and egg mass to produce egg mass estimates for over 5,500 species previously lacking such information. These estimates are accompanied by measures of the robustness of the regressions used to produce them (e.g., sample size, root mean square error [RMSE] of estimation, coefficient of determination, and degree of extrapolation), thus allowing independent evaluation of the suitability of any estimate to address a particular research question relating to avian life history. Most estimates (~5,000) were based on family-level egg mass–body mass regressions, with the remainder derived from other relationships such as ordinal regressions. We compared estimating regressions based on adult vs. female body masses and, after finding little difference between the 2, based our final estimates on adult masses as those were more numerous in the literature. What small differences between adult- and female-based regressions that did occur were not related to sexual size dimorphism across families. These new estimates, coupled with ~5,000 egg masses reported in the literature, provide a foundation of over 10,000 species for wider investigations assessing variation in reproductive effort in birds over a broad array of ecological and evolutionary contexts.

Keywords: allometry, body mass, egg mass, reproductive effort, sexual size dimorphism

LAY SUMMARY

- The mass of a bird's egg is a critical attribute of the species' life history but has not been reported for the majority of avian species.
- We capitalized on the strong statistical relationship between egg mass and avian body mass (known for almost all bird species) to produce new egg mass estimates for over 5,500 species previously lacking such information.
- Most estimates (~5,000) were based on family level regressions of egg mass on body mass, with the remainder derived from other relationships such as order regressions.
- We found little difference between egg mass relationships calculated from adult vs. female-only body masses and based our final estimates on adult masses as those were more numerous in the literature.
- These new estimates, coupled with ~5,000 egg masses reported in the literature, provide a foundation of over 10,000 species for wider investigations examiniing variation in reproductive effort in birds over a broad array of ecological and evolutionary contexts.

Estimación de las relaciones entre masa del huevo y masa corporal en las aves

RESUMEN

La masa del huevo de un ave es un atributo clave de la historia de vida de la especie y representa un componente fundamental del esfuerzo reproductivo. En efecto, la solución de compromiso entre el número de huevos en una nidada y la masa de la nidada es una de las preguntas centrales para entender cómo los atributos ambientales como la depredación del nido o la mortalidad de los adultos influencian la inversión reproductiva. Sin embargo, las masas de los huevos no han sido reportadas para la mayoría de las especies de aves. Aprovechamos la fuerte relación alométrica entre la masa corporal de las aves y la masa del huevo para producir estimaciones de la masa del huevo para más de 5500 especies para las que anteriormente no se tenía esta información. Estas estimaciones están acompañadas por medidas de la robustez de las regresiones usadas para producirlas (e.g., tamaño de muestra, raíz del error cuadrático medio de la estimación, coeficiente de determinación, grado de extrapolación), permitiendo por ende una evaluación independiente de la pertinencia de cualquier estimación para encarar una pregunta particular de investigación relacionada con la historia de vida de las aves.

La mayoría de las estimaciones (~5000) estuvieron basadas en regresiones entre la masa del huevo a nivel de familia y la masa corporal, con las restantes derivadas de otras relaciones como regresiones ordinales. Comparamos estimaciones de regresiones basadas en las masas corporales de adultos vs. hembras, y luego de hallar poca diferencia entre las dos, basamos nuestras estimaciones finales en las masas de los adultos, ya que eran más numerosas en la literatura. Las pequeñas diferencias entre las regresiones de adultos y hembras que ocurrieron no se relacionaron con el dimorfismo de tamaño por sexo entre las familias. Estas nuevas estimaciones, junto con ~5000 masas de huevos reportadas en la literatura, brindan una base de más de 10,000 especies para realizar investigaciones más amplias que evalúen las variaciones en el esfuerzo reproductivo de las aves a través de una amplia gama de contextos ecológicos y evolutivos.

Palabras clave: alometría, dimorfismo de tamaño por sexo, esfuerzo reproductivo, masa corporal, masa del huevo

INTRODUCTION

The mass of a bird's egg is a fundamental attribute of the species' life history. Variation in egg mass among species is related to incubation period (Rahn and Ar 1974, Deeming et al. 2006), hatchling mass (Deeming and Birchard 2007), water vapor conductance and water loss from the egg (Ar et al. 1974, Rahn and Paganelli 1990, Birchard and Deeming 2015), and oxygen consumption pre-hatching (Rahn and Paganelli 1990, Birchard and Deeming 2015). Within a species, larger eggs are associated with increased hatching success, and generally result in larger and heavier chicks that have increased growth and survival (Krist 2011). When multiplied by the number of eggs in the clutch of a species and the number of clutches per year, egg mass becomes part of an important metric of reproductive effort, clutch mass (e.g., Martin et al. 2006, Balasubramaniam and Rotenberry 2016). One of the basic predictions of life history theory is a tradeoff between egg mass and clutch size, presumably driven by partitioning a fixed amount of resources between the number of offspring in a breeding event and their size (Roff 1992). To the extent that other environmental attributes, such as nest predation or adult mortality, influence reproductive investment, a species' location along the tradeoff gradient, and hence egg mass, may shift. For example, increased nest predation generally favors reduced reproductive investment, which may be manifest in reduced clutch size (e.g., Slagsvold 1984). However, to the extent clutch size trades off with egg mass, nest predation might indirectly influence egg mass by directly affecting clutch size (Martin et al. 2006). Egg mass may also vary among species differentially distributed along physical gradients; for example, in Galliformes egg mass declines with latitude but increases with elevation, presumably in response to variation in resource availability due to physical attributes that globally vary across the 2 geographical extents (Balasubramaniam and Rotenberry 2016).

Another fundamental property of a bird's egg mass is its allometric relationship to body size across species (Rahn et al. 1975); indeed, a predictive egg mass–body mass relationship extends into the avian fossil record (Dyke and Kaiser 2010). This relationship is customarily derived by regressing log-transformed egg mass on log-transformed body mass; the slope of this regression is the scaling exponent (the relative rate of change of egg mass with respect to the rate of change of body mass) and its intercept is the normalization constant (Niklas and Hammond 2019). Most often the scaling exponent (or "allometric coefficient") is less than 1, implying that relatively larger birds have relatively smaller eggs. However, this exponent is not uniform, but instead can vary considerably among groups of species based upon phylogeny (Deeming 2007a, b), parental incubation behavior (Martin et al. 2006, Varricchio et al. 2008; but see Birchard et al. 2013), developmental mode (Deeming 2007a, b, Dyke and Kaiser 2010, Birchard and Deeming 2015), and sexual size dimorphism (SSD) (Olson and Cockburn 1993, Weatherhead and Teather 1994). This further implies that selection pressure on any of these traits may in turn create selection pressure on body mass, producing complex feedback among, and indirect effects on, other life history attributes, including egg mass (Sæther 1987, Martin et al. 2006). For example, Olson and Cockburn (1993) observed, among other things, that in species where the female was the larger sex, the more dimorphic species had relatively small eggs for the mass of the female; conversely, species with larger males had relatively large eggs. They concluded that their results were consistent with the hypothesis that patterns of size dimorphism in predatory birds (which frequently manifest size dimorphism and were abundant in their sample) are determined by sexual selection. Thus, sexual selection on body size may indirectly influence egg mass.

It is clear, then, that the mass of a species' egg is deeply embedded in the evolutionary processes that shape avian life histories and in the ecological processes that influence species' distributions. Unfortunately, the egg masses of the majority of avian species have not been reported (only 4,916 out of our sample of 10,493 species; see Data Sources below). However, the body mass of the great majority of birds (10,432 of 10,493) is known and readily available (see Data Sources below). This suggests that we should be able to capitalize on the allometric relationship of egg mass to body mass to generate reliable estimates of egg mass for many of those species for which it is currently lacking. Moreover, as the species we analyze span virtually the entire avian phylogeny, we lay the groundwork for interpreting variation in egg mass across a broad array of ecological or evolutionary contexts.

Our principal aim is to assemble and expand the dataset (egg masses) that forms the foundation for testing hypotheses

set in the framework of life history evolution and ecology. We begin by describing the sources of egg mass data taken from the literature; our analyses would not be possible without the extensive work of others, whom we gratefully acknowledge. From those data we develop regression models that allow us to estimate egg mass from body mass so that we can fill in missing values. We take adult mass as our metric of body mass, and demonstrate its advantages over using female mass (see Adult Body Mass vs. Female Body Mass, and SSD below). Insofar as possible we preferentially partition egg mass–body mass regressions by family, but employ alternative approaches (e.g., ordinal-level regressions) in cases where family-level regressions proved unsuitable (less than 9% of species). We produce a table of regression coefficients for each family and order (which we compare with those generated by Rahn et al. 1975, 1985), and a table of reported or estimated egg masses for 10,432 species.

METHODS

Data Sources

Our principal source of adult body mass data was "Amniote," a dataset assembled by Myhrvold et al. (2015). For species missing data in Amniote we turned to "Elton," assembled by Wilman et al. (2014). Both datasets drew body masses primarily from Dunning (1992) and numerous handbooks and field guides, as well as primary literature. We elected to use "adult" rather than "female" body masses in our regressions, a choice we rationalize below (see Adult Body Mass vs. Female Body Mass, and SSD).

Amniote was also our principal source of egg mass data; for those species still missing data we examined entries in the Handbook of Birds of the World Alive (HBW hereafter; del Hoyo et al. 2017). For species with multiple underlying values in the literature for egg mass and/or body mass, Amniote reports the species' median.

We based our taxonomy on the International Ornithologists' Union World Bird List Version 9.2 (IOC hereafter; Gill and Donsker 2019). This list yielded 10,493 species distributed among 248 families in 40 orders. Where species taxonomy from life history sources differed from the IOC, we aligned the sources with the IOC list by using a comparison of the IOC with other world lists provided by Gill and Donsker (2019). Although the IOC taxonomy guided our initial partitioning of species into separately analyzed units (families, orders), in some cases (noted below) we combined 2 or more units for generating predictive equations.

Cleaning the Data

As an initial check, we regressed (using ordinary least squares [OLS] regression) untransformed body mass values from Elton on those from Amniote for the 8,925 species that appeared in both datasets. Not surprisingly, since both relied on similar sources, the r^2 was high (0.997) with a slope near one (0.997) and an intercept near zero (0.002). However, we identified several outliers (species with large residuals) that we suspected represented data entry errors, which we corrected when possible based on the HBW, or deleted. Similarly, we searched for outliers by examining each plot of the initial regression of egg mass on body mass (both variables $\log_{10}$-transformed) for each family and each order (although family was our principal taxonomic level for analysis, not all families had sufficient numbers of species with data to generate meaningful regressions). Again, we looked for species with noticeably large residuals and sought independent assessment of the quality of their data in the HBW. After dealing with any outliers, we re-ran the regressions and used the results to estimate egg mass for those species for which it was initially missing. We then produced plots of both actual and estimated egg masses vs. body mass, and again examined them for outliers associated with the estimated data. We also looked for species with exceptionally large or small egg or body masses compared with the majority of species within their taxonomic group, and again sought independent confirmation of their measurements. Subsequent to final corrections, we performed the final regressions and created the final egg mass estimates for those species previously lacking them. Several ratite genera (*Struthio*, *Rhea*, and *Casuarius*) had inconsistent body mass and egg mass values across Amniote, Elton, and the HBW. For these we consulted Davies (2002). A list of all changes to the original Amniote data appears in Supplementary Material Table S1.

Regression Analysis

We generated estimates of the scaling exponent and the normalization constant in the usual way, by regressing $\log_{10}$-transformed egg mass on $\log_{10}$-transformed adult body mass. For generating predictive equations, OLS regression of egg mass on adult body mass is most suitable, regardless of whether the predicting ("independent," or X) variable is measured with error (Legendre and Legendre 1998, Warton et al. 2006, Smith 2009). Such a regression line has fitted Y ("dependent" variable) values as close as possible to the observed Y values, which is desirable if we are simply interested in predicting Y values given a set of X values. For the purposes of prediction, we assess fit using both r^2 and the RMSE (the square root of the variance of the residuals). Whereas r^2 is a relative measure of fit, RMSE is an absolute measure; the former is a familiar statistic representing the proportion of variation in one variable statistically explained by another, whereas the latter is a measure of how accurately the regression model predicts the response.

As noted above, after cleaning the data we performed OLS regression of $\log_{10}$-transformed data family by family, using each species as an independent data point. We examined each family-level regression and assessed its suitability for estimating egg mass based on a combination of sample size, r^2, and RMSE. Criteria were not rigid; for example, we deemed suitable a regression based on a small sample size if the RMSE was also arbitrarily small (~0.1 or less), particularly if the sample represented the majority of species in the family. If deemed suitable (we indicate in regression results which families were so), we applied the equation to those species missing egg mass. We plotted the results (original data plus the new estimates) and again looked for large residuals suggestive of potential data errors, which we corrected when necessary, then re-ran to generate the final regression coefficients.

The shared ancestry of hierarchically related species will often produce phenotypic similarities, clearly violating the notion of statistical independence and thus compromising ordinary statistical tests in comparative analyses (Felsenstein 1985). To account for this lack of independence, a variety of methods have been developed that explicitly take into account phylogenetic relationships (e.g., Martins and Hansen 1997, Freckleton et al. 2002, Adams and Collyer 2018), and such phylogenetic "control" or "correction" is now frequently applied. However, the need for phylogenetic correction is not an issue here. As Pagel (1993) and Rohlf (2006) demonstrate, the slope of the ordinary (uncorrected) regression of one trait on another is an unbiased estimate of a slope of the relationship that takes into account phylogenetic relationships. Rohlf (2006) further shows through simulations that slopes of both OLS and phylogenetic generalized least squares essentially mirror the parametric values used to generate the simulations. Both Pagel (1993) and Rohlf (2006) observe that the lack of independence of observations sampled across a phylogeny has its effect on estimates of sample variance and standard error (it causes them to be underestimated), leading to a larger number of type 1 errors in statistical tests. Thus, the coefficients we generate to estimate egg mass from body mass are unbiased, and adding a phylogenetic framework will not alter them. In this particular case, robustness of our individual species' egg mass estimates and the regression coefficients used to derive them are indexed by the sample size, regression r^2, RMSE of estimation, and any degree of extrapolation, all of which we provide.

In cases where family-level regressions were deemed unsuitable for estimation (most frequently due to small sample sizes), we used one of several alternative approaches. We indicated in the results for each species which of these alternatives was used. For example, 10 families had species whose known body masses and egg masses fell into a relatively narrow range, which produced regressions with low r^2. Thus for 26 species in 11 genera we used genus averages to estimate their egg masses. Similarly, in one case (Mesitornithidae) we used the family average egg mass as an estimate for 2 species, and in another case (Modulatricidae) we used a related family (Promeropidae; Johansson et al. 2008) average as an estimate for 3 species. In all cases the body masses of the species whose egg mass was being estimated was similar to that of the species being used for estimation.

In 4 cases we combined closely related families to generate regression equations for members within each family: (1) a "barbet" regression combining Capitonidae, Lybiidae, Megalaimidae, and Semnorithidae (morphologically similar and until recently lumped into a single family under the first name; Short and Horne 2019); (2) a "bombycillidae sensu lato" combining Bombycillidae, Dulidae, Hylocitreidae, Hypocoliidae, and Ptilogonatidae (the latter 2 at one time considered subfamilies of the first; Spellman et al. 2008); (3) a "broadbill" regression combining Eurylaimidae, Calyptomenidae, Sapayoidae, and Philepittidae (morphologically similar and until recently lumped into a single family under the first name; Moyle et al. 2006); and (4) a "Galbuli" regression, recognizing consideration of Galbulidae and Bucconidae as a distinct suborder within the Piciformes (e.g., Ericson et al. 2006).

As noted above, egg masses for ratites were inconsistent across our principal sources of information, and therefore we used masses reported by Davies (2002). We also divided cuckoos (Cuculiformes: Cuculidae) into brood-parasitic and non-parasitic species (Supplementary Material Table S2; Payne 2005, 2019) and performed separate regressions for each (Supplementary Material Figure S2).

Thirty-five additional families either had insufficient numbers of species with reported egg masses or unsuitable regressions ($r^2 < 0.6$) to use as estimators, for which we instead used alternative methods. Our principal approach was to use a related, morphologically similar family with a satisfactory regression equation that also had an appropriate range of egg and body masses. In cases where a family had been created in a recent taxonomic revision but lacked a clear, closely related family, we used the original family from which the species in the newer family had been extracted. We ultimately used related or former families for 168 species in 20 families (see Supplementary Material Table S3 for surrogate taxa). In other cases, however, this was not possible. For example, of the 20 species in the families Aegothelidae, Hemiprocnidae, and Nyctibiidae, only 4 had known egg masses. For these taxa we used a regression based on combining all species in Apodiformes and Caprimulgiformes to capture the range of morphological variation in these families (Supplementary Material Figure S2). Likewise, only 4 of 43 species of

toucans (Ramphastidae) had reported egg masses. Within Piciformes, toucans are in a clade with barbets (Prum et al. 2015), but are much larger (toucans average 263 g whereas barbets [4 families] average only 62 g), rendering the latter undesirable for regression estimation. Piciforms, excluding toucans, average 72 g, with little overlap in size ranges. Thus, to avoid excessive extrapolation, for Ramphastidae we used the overall Class Aves regression to estimate their egg masses. Because Cariamidae is not closely related to other families or orders, we also used the Aves regression to estimate the egg masses of the one species with an unreported egg mass in this family/order. Finally, for 22 species in 10 families in 2 orders we could not find suitable related families and ultimately used ordinal regressions.

Extrapolation

The body masses of some species without egg masses lay outside the body mass range over which their relevant regression was performed, and thus their estimated egg masses based on those regressions represent extrapolation. In many cases the extrapolation was slight (that is, the body mass was only marginally outside the regression body mass range), and it seems likely that the estimates are reliable (i.e. the case to be predicted still lies within the domain of the regression; Smith 2009). Nonetheless we noted each case of extrapolation in the results, and we provided a quantitative index of the degree of extrapolation, expressed as the proportional extension of the regression line past the last observed value used in calculating the regression. This "proportional extrapolation" is simply the difference between the body mass of the maximum (or minimum) observation used in the regression and the body mass for which egg mass is being estimated, divided by the range in body mass over which the regression is calculated. To illustrate: body mass values used in the regression for Accipitridae ranged from 84 g (*Accipiter mimullus*) to 10,000 g (*Gyps himalayensis*), a span of 9,916 g. Log_{10}-transformed, these values are 1.9245 and 4.0000, a span of 2.0755. The body mass for *Accipiter superciliosus*, whose egg mass we wish to estimate, is 73.9 g, or $\log_{10} = 1.8686$. This value represents an extension of 0.0559 beyond the minimum used in the regression (1.9245–1.8686), and is a proportional extension of the original range of 0.027 (0.0559/2.0755), or less than 3%. We consider this extrapolation to be sufficiently slight that we would include this species' estimated egg mass in further analyses. To provide the relevant context, we also report the minimum and maximum body masses over which each regression was calculated (Niklas and Hammond 2019).

RESULTS AND DISCUSSION

Our roster of 10,493 species represented 40 orders and 248 families (Supplementary Material Table S4 and Figure S1). We ultimately obtained 9,401 adult body masses from Amniote and 1,022 from Elton; 70 species lacked body mass information, although 9 of those had reported egg masses. Amniote provided 4,829 egg masses and we extracted an additional 91 from the HBW. Seven orders and 88 families had less than 3 species with egg masses, and thus no regression estimate could be calculated, although in many cases the single or both species in the taxon had published values. Not surprisingly, the remaining 193 possible regressions varied considerably in terms of their quality as indexed by RMSE (Supplementary Material Table S5). We deemed 122 family-level regressions as acceptable for estimation, all but 3 with RMSE ≤ 0.100 (Supplementary Material Figures S2 and S3). These 122 regressions had an average RMSE = 0.053 (standard deviation [SD] = 0.021), average $r^2 = 0.834$ (SD = 0.156), and used a total of 4,514 species with reported egg masses to generate estimated egg masses for an additional 5,031 species. In 2 additional families, each with 2 species of known masses, we used simple interpolation as body masses for species with unknown egg masses lay in between. Including all sources (literature and estimation), we ultimately generated egg mass values for 10,432 species (Table 1, Supplementary Material Table S4). Notably, there was considerable variation among families with respect to the regression coefficient, implying substantial scope for associated life history trait variation related to egg size and body size. For the 105 families for which there were at least 10 species with egg mass data, regression coefficients ranged from 0.335 to 1.022. We note, however, that although we used what we considered the best estimation procedure for each taxon in the context of the data available, due to inadequate sample size, weak regression (i.e. low r^2 and/or RMSE), extrapolation beyond the limits of a regression, or selection of an inappropriate surrogate taxon, some estimates (egg mass and/or regression coefficient) may be considered unreliable. Therefore, we provide information relevant to each of these criteria to allow independent assessment of the reliability of each species' estimate and its appropriateness for use in any particular research application (Supplementary Material Tables S4 and S5).

Although most analyses of allometric relationships focus on the slope of the relationship within and across taxa, a second variable, the regression *Y*-intercept (or normalization constant), also showed substantial variation. Although obviously a critical component to estimating values of the dependent variable, its direct interpretation is more problematic due to what Niklas and Hammond (2019) call the range of applicability problem. We note that in all cases in these data, the *Y*-intercept lay well outside the range of data values used to generate the regression equations (i.e. all body masses were >1 g, or $\log_{10} = 0$), and thus any

TABLE 1. Sources for egg masses reported in Supplementary Material Table 4

Source	Number of species
No estimate, lacking body mass information	61
Egg mass from literature (Myhrvold et al. 2015, del Hoyo et al. 2017)	4,916
Class regression	40
Ordinal regression	23
Family regression	5,030
Genus average	26
Family average	2
Related family average	3
Davies (2002)	4
"Apod + Capri" (ordinal, Apodiformes + Caprimulgiformes) regression	16
"Bombycillid sensu lato" (Bombycillidae + Hylocitreidae + Ptilogonatidae) regression	5
"Barbet" (Capitonidae + Lybiidae + Megalaimidae + Semnornithidae) regression	52
"Broadbill" (Eurylaimidae + Calyptomenidae + Sapayoidae + Philepittidae) regression	15
"Galbulae" regression (Galbulidae + Bucconidae)	49
Brood-parasitic and non-parasitic Cuculiformes regressed separately	28, 55
Regressions based on related families (see Supplementary Material Table S3)	168
Total	10,493

interpretation or analysis of its value implicitly involves extrapolation and its associated uncertainties. Thus, if one wishes to compare the offset of 2 regressions that might otherwise have the same slope, we suggest following Rahn et al. (1975) in calculating for each regression their values at one or more fixed body mass values (e.g., 10 g, 100 g) falling within the observed range of values for the regressions of taxa to be compared.

Comparison with Rahn et al.

Although Rahn et al. (1975, 1985) published egg mass–body mass regression coefficients for a number of taxa, a straightforward comparison of our coefficients with theirs is compromised by the fact that several of their orders combined families that are no longer considered to be in the same order, and therefore not evaluated by us (e.g., they combined Accipitridae and Falconidae in Falconiformes, but did not provide family-level regressions for either). Moreover, they used female body mass whereas we used adult body mass, although we show below that this difference has a relatively small effect. Nonetheless, the correlation between their coefficients and ours for the 10 orders we shared was 0.568 (Figure 1A), with Galliformes and Piciformes as the most notable differences. These differences were primarily due to the greater among-family heterogeneity that was included in our analysis (see Ordinal vs. Family Regressions below). For 28 comparable families, the correlation was 0.588 (Figure 1B). Notable outliers were Pycnonotidae and Troglodytidae; although we are tempted to conclude that the difference is due to the much greater sample size in our data (49 vs. 17 for the former family, 16 vs. 8 for the latter), other families such as Strigidae also had much greater numbers in our data (86 vs. 15) with essentially no difference.

Ordinal vs. Family Regressions

Although a number of other studies investigating egg mass–body mass relationships in birds have reported and relied upon ordinal-level regressions for inference (e.g., Rahn et al. 1975, Sæther 1987, Deeming 2007a, b), our analyses pointed out a potentially serious problem in doing so: an ordinal-level regression may mask substantial heterogeneity among family-level relationships, which in turn may yield an ordinal coefficient that differs substantially from one or more or even all of the family ones. In other words, egg mass–body mass relationships can exhibit phylogenetic scale-dependency (Graham et al. 2018). This pattern was particularly conspicuous in Galliformes, where there was an almost doubled difference between the largest and smallest family-level regression coefficients (0.986 for Odontophoridae vs. 0.505 for Megapodiidae), and the average absolute difference in family regression coefficients compared with the ordinal regression coefficient was 0.188, with a range of 0.126 to 0.308 (Figure 2). Birchard and Deeming (2015) show a virtually identical pattern relating egg energy content (closely related to egg mass) to body mass in Galliformes (their figure 9.4b). The implications for estimation of egg mass are obvious; whereas the average RMSE for the 5 family-level regressions was 0.066 (SD = 0.016), that for the ordinal-level regression was 0.194 (Supplementary Material Table S5).

This pattern arises less because the family slopes differ (although in this case they do somewhat), but more because the family means are offset; indeed, even if family slopes are identical, if centroids are sufficiently offset an overall regression coefficient can be substantially different from the individual ones, even to the point of differing in sign. Thus, conclusions based on one taxonomic scale may not hold for another scale (Graham et al. 2018). This

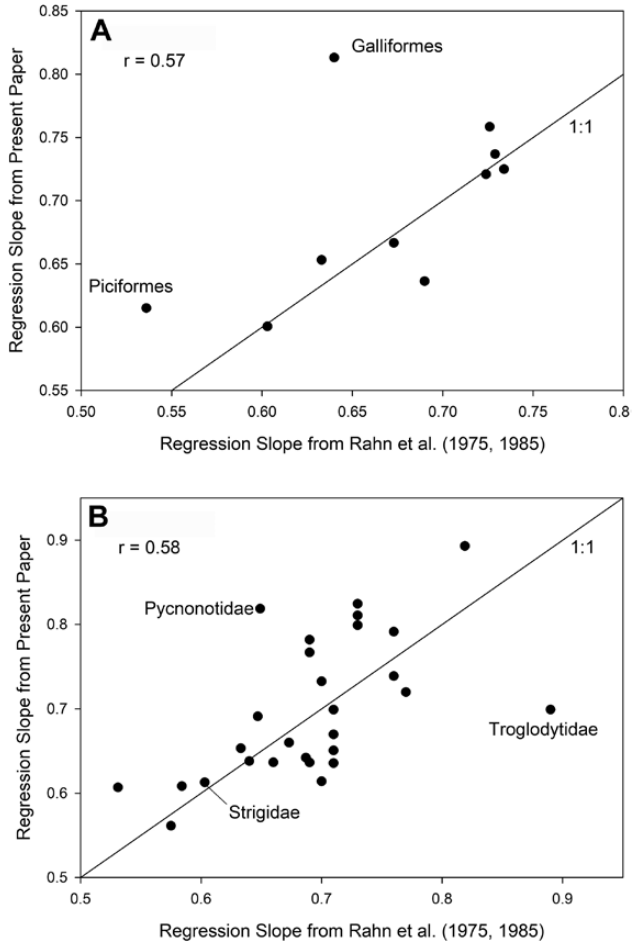

FIGURE 1. Comparison of slopes of egg mass–body mass relationships resulting from ordinary least squares regressions taken from Rahn et al. (1975, 1985) and those reported here, for orders (**A**) and families (**B**). Solid line denotes one-to-one relationship between slopes; taxa mentioned in text highlighted.

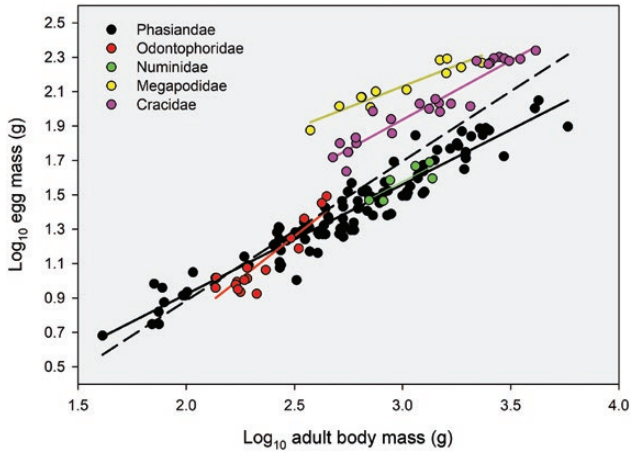

FIGURE 2. Egg mass–body mass relationships for families within Galliformes. Solid lines denote ordinary least squares regressions for each family; dashed line is regression based on all species. Regression slopes are: Galliformes, 0.813; Phasianidae, 0.683; Odontiphoridae, 0.986; Numididae, 0.654; Megapodiidae, 0.505; Cracidae, 0.687.

phenomenon in life history analysis has been referred to as the "big car-big house" problem (Reznick et al. 2000, Careau and Wilson 2017). The pattern can arise not only with respect to families within orders, but potentially orders within a class, or genera within families. This leads to the question of which level is best for allometric analysis? We elected to use family because diversification at that level accounts for over 90% of the total variation in several life history traits associated with reproductive effort in birds (Owens and Bennett 1995). Likewise, in their analysis of egg allometry in the context of the altricial-precocial continuum in birds, Birchard and Deeming (2015) suggest that analysis at the family level (they used the term "grade") was more appropriate than at the order level because variation in the former confounded results from the latter, as we both observed in galliforms. Our analysis of galliforms implies that a simple diagnostic of whether within-taxon heterogeneity is potentially an issue is to compare RMSEs for within-level regressions (e.g., families within an order) with that for the across-level regression (the order); if the latter is several times higher (e.g., 3 times higher in our galliform example), then further investigation may be warranted. Other orders with conspicuous within-taxon heterogeneity included Charadriiformes, Gruiformes, Suliformes, and Passeriformes (Supplementary Material Figures S2 and S3).

Adult Body Mass vs. Female Body Mass, and SSD

It is often assumed that any allometric relationship between egg size and avian body size is a consequence of the mechanics and physiology associated with the egg's development, transportation, and laying, and is thus largely a product of female body mass (Weatherhead and Teather 1994). For this reason, many analyses of egg allometry are restricted to female mass variation (e.g., Rahn et al. 1975, 1985, Dyke and Kaiser 2010), which can be further rationalized as an avoidance of issues of SSD, where males and females may differ significantly in body mass (e.g., Birchard and Deeming 2015). However, there are several reasons why adult body mass is a desirable metric for predicting egg masses and examining egg allometry.

As noted above (Methods), the choice of an independent variable in developing a predictive equation is not strictly constrained by imputing a specific functionality to its relationship with a dependent variable. However, calculating allometric coefficients does posit some sort of functional relationship between 2 variables, and because females develop, transport, and lay eggs, egg size is often assumed to be a female trait. However, Weatherhead and Teather (1994) observed that male size influenced egg size across

a spectrum of SSD, as did Olson and Cockburn (1993) and Olsen et al. (1994). Weatherhead and Teather (1994) suggest that this result should be expected. They point out that females inherit the genetic basis for the eggs they lay from both mother and father, and that these heritabilities can be relatively high and similar whether based on maternal (0.57) or paternal (0.48) half-sib correlations (heritabilities for domestic chickens, summarized in Kinney 1969). Moreover, they note that the effects of any paternal genes for egg size will be expressed in their daughters, and therefore exposed to natural selection. Thus, egg size can evolve directly as a function of both male and female traits (i.e. body mass), and adult mass (whether arithmetic or geometric mean of the 2 sexes; Olson and Cockburn 1993) is a relevant metric for considering allometric variation in egg size.

Because we have over 4,000 species with female body masses from Amniote paired with reported egg masses, we can also examine the practical consequences of using adult vs. female masses in predictive (OLS) regressions. First, we observe that the differences in female-based vs. adult-based OLS regression results were small. There were 93 families from Amniote with at least 10 species with both female and adult body masses, and corresponding egg masses; the correlation between the regression slopes for these families was 0.883 (Figure 3A; Supplementary Material Table S6). The average slopes for both types of regression were virtually identical (female = 0.683, adult = 0.678; SD = 0.118 and 0.113, respectively), and the average absolute difference between slopes across all families was 0.043 (SD = 0.037; Supplementary Material Table S6). The correlation between intercepts was 0.951. Both independent variables achieved the same precision of estimation, with an average absolute difference in RMSE of 0.007 (SD = 0.007) over average female RMSE of 0.059 (SD = 0.025) vs. average adult RMSE of 0.060 (SD = 0.025).

Second, we note that we have 5,636 female body masses, 4,215 of which are paired with an egg mass. Even if all of these generate satisfactory regression equations, we can only estimate egg masses for species missing egg mass data for a maximum of the 1,421 additional species for which we have female mass (not all taxa will have usable regressions due to small sample size or poor fits). Alternatively, we have 10,478 adult body masses, a potential increase of over 4,800 additional species compared with using females only.

Variation in SSD among these 93 families was substantial and has been observed to affect female body size–egg size relationships (Olson and Cockburn 1993, Olsen et al. 1994, Weatherhead and Teather 1994). We estimated SSD for each species by subtracting $\log_{10}$ female body mass from $\log_{10}$ male body mass (essentially the ratio of the 2 untransformed masses) for the 4,487 species from

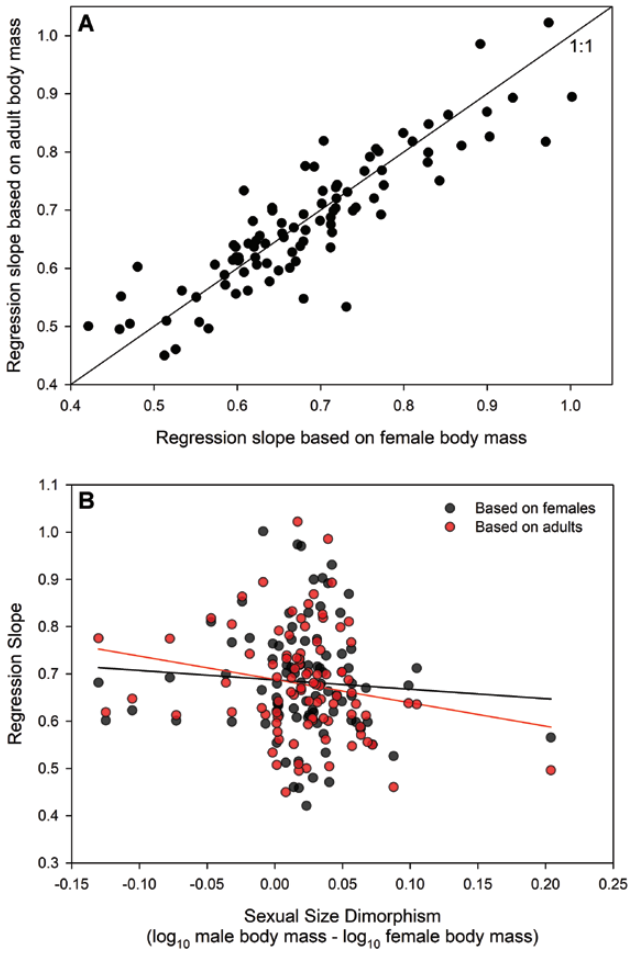

FIGURE 3. Comparison of slopes of egg mass–body mass relationships resulting from ordinary least squares regressions based on female body mass with those based on adult body mass for 95 families with at least 10 species with female body masses (**A**), and their relation to sexual size dimorphism (**B**). Solid line in (**A**) denotes one-to-one relationship. Solid lines in (**B**) denote separate regressions based on females and adults.

Amniote for which there were both values, then averaged these within families (minimum of 10 species). Although the overall average SSD = 0.020 (equivalent to a <5% difference in absolute mass), it ranged from –0.130 to 0.204 (Supplementary Material Table S6). The top 5 male-biased families (SSD > 0.07) were Otididae, Icteridae, Phasianidae, Paradisaeidae, and Bucerotidae, whereas the most female-biased families (SSD < –0.07) were Turnicidae, Accipitridae, Falconidae, Tytonidae, and Strigidae. However, variation in SSD appeared to have essentially no relation to the predictive slope based on female masses (r = –0.075), and a small, negative association with the slopes based on adult masses (–0.194; Figure 3B). The differences (absolute) in slopes generated by females vs. adults were not associated with SSD (r = 0.037).

CONCLUSIONS

To conclude, these estimates provide an expanded foundation for wider investigations into the evolutionary processes driven by variation in reproductive effort, and their role in molding other aspects of avian life histories. For example, egg mass is frequently used as an index of parental investment in precocial species (Starck and Ricklefs 1998, Martin 1987). Overall, it can have a significant effect on the post-hatching condition and survival of chicks in both precocial and altricial species (Krist 2011). Likewise, increasing egg mass is associated with increasing oxygen consumption and water loss from the egg (Birchard and Deeming 2015) and, thus, must be taken into consideration in any examination of reproductive trait variation along elevational gradients (Balasubramaniam and Rotenberry 2016). As incubation period generally increases with egg mass (Rahn and Ar 1974, Deeming et al. 2006), to the extent that the probability of nest loss to predation increases with time of exposure suggests complex tradeoffs among egg mass and clutch size, potentially influencing body mass as well. Moreover, considering just those species for which we have literature-based values for egg mass, 4,275 have associated clutch size information necessary for estimating clutch mass (J. T. Rotenberry and P. Balsubramaniam personal observation assembled from Amniote, Elton, and the HBW). With regression-based estimates we add up to 3,622 more species with both egg mass and clutch size data, an increase of over 80% in our ability to estimate this critical component of reproductive effort (Martin et al. 2006).

It was clear that there was substantial variation in allometric coefficients among orders, among families within orders, and even between orders and their families. This suggests the prospect that different processes are important at different taxonomic scales, as observed in avian egg shape evolution (Birkhead et al. 2019, Stoddard et al. 2019). In that example, Stoddard et al. (2017, 2019) performed a class-wide analysis that concluded that, over a broad phylogenetic scale that spanned 34 orders, adaptations for flight might be important drivers of egg shape variation. However, within each of 2 families of distantly related but ecologically similar species (Alcidae and Spheniscidae), Birkhead et al. (2019) observed that incubation site explained the majority of variation in egg shape. Likewise, although SSD had little effect on the differences in regression coefficients based on females or on adults over 95 families considered at once, the wide range in SSD within families and among orders implies we should not ignore its potential importance in influencing allometric relationships in some taxa. Finally, we hope the observation that egg masses have not been reported for over half the extant species of birds will encourage ornithologists working in the field to collect and publish this and other life history attributes (e.g., clutch size, clutches per year) so that we can replace estimates with true values.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *The Auk: Ornithological Advances* online.

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